Action in the brain

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Introduction

If we stop our busy life for a minute and take a look around us, we see that the world is full of wonders and, in particular, we realize that it is full of other human beings. What strikes me most, is how easily we understand each other, and how communication sometimes works best without words. Of course we also misinterpret each other, but these errors might help us unravel the rules we normally use to understand each other.

It is with this awe that I started studying biology and that my enthusiasm flourished when I heard about the discovery of the Mirror Neuron System (MNS). In 1996, Vittorio Gallese, Leonardo Fogassi, Giacomo Rizzolatti and colleagues discovered, in the macaque premotor region F5, a set of neurons discharging both when the monkey performed an action (e.g. grasping a piece of food or breaking a peanut) and when the monkey saw the experimenter executing the same action (Gallese and others, 1996). Described in such a simple sentence, mirror neurons might appear to be 'just' another type of multi-modal neurons, integrating visual and motor properties — but again, if we stop and think for a minute, this 'double' activation could provide us with an elegant way for understanding the behavior of the people that surround us: we would immediately share their actions. Before continuing along this enticing interpretation, and share with you the questions I tried to answer in these three years, in the first chapter of my thesis, I will review, together with my supervisor, some of the most important concepts about the MNS, including the key brain regions involved, the evidences for its presence in humans, its likely involvement in language acquisition, how it possibly emerges, and importantly, we will review evidences for the existence of a similar system for sensations and emotions. Finally we will underline its limitations and offer a hypothesis, described in more details in chapter two, of how it could integrate with a more disembodied and deliberate mentalizing about other people (theory of mind,ToM)[1].

At the commencement of my PhD work, many aspects of the MNS were (and unfortunately of these many still remain) poorly understood. In chapters 3 to 6, the empirical core of this thesis, I will address some of these questions, focusing on the human MNS.

The MNS is claimed to translate observed actions into a motor representation of corresponding actions. But what aspect of the action is really represented in these corresponding motor programs? Is it the way in which the action is performed or what is performed? In Chapter 3 I examine these alternatives and suggest that in cases where the details of the action cannot be matched, the goal can be sufficient to recruit the MNS. Chapter 4 will further stress the sufficiency of goals for the MNS: we found that aplasic individuals, born without arms or hands, activate their MNS to the same extent as typically developed participants while observing actions performed with hands. Aplasic individuals perfectly knew what the agent was trying to achieve, because they usually accomplish it with their mouth or feet. The fact that the observed action was performed with a hand wasn't enough to prevent the mirror activation.

If the MNS is indeed an important tool for understanding the actions of other people, we might expect to find a MNS in each and every human individual. Traditionally, fMRI studies of the MNS use group analyses that combine the data of all the subjects. In contrast, in Chapter 5 I will adopt a single subject perspective, examining the presence of this system in each participant. In addition, I will try to quantify and compare the relative contribution of distinct brain areas to the MNS in order to provide a more objective description of the anatomy of the MNS.

In chapter 6 I will explore three additional aspects of the MNS. First, we checked whether the sound of an action is, also in humans, sufficient to recruit the MNS. Auditory responses in the human MNS would further strengthen the role played by goals in action understanding: the sound of an action clearly does not indicate the way in which the action is performed (whether you open a bag of chips with both hands, or with a hand and the mouth would cause the same sound). Second, we explored the relationship between goal and effector matching by exploring the somatotopical nature of mirror responses. Finally, we explored the relationship between the MNS and empathy by examining whether differences in activations correlate with inter-individual differences in empathy questionnaires.

I believe in science answers and questions go hand in hand: you start with a simple question and the answer you gain opens the way to many new questions, resulting in a dauntingly never-ending process. Once in a while, though, we should stop and think about what we have done so far and what we could do next, and this thesis represents just one of these moments. These three years helped me in sketching a first outline of the neural basis of our understanding of the actions and sensations of other individuals. In my last chapter I will therefore briefly summarized what we have found and believe, until now, about these circuits. This is not my final answer, but a good moment to stop and think.

General, but important remarks

There are a couple of important points I would like to discuss before the next chapters. One of them underlines an important aspect of the thesis that might otherwise remain hidden. The other three, I hope, will help clarify some aspects that would otherwise remain ambiguous.

Repeated Measurements of the Same Subjects

Most of my experimental work is based on the same pool of subjects, tested under different conditions. This approach enables the direct comparison of different experiments. It for instance enables the comparison of the locations involved in observation, listening and execution of actions in the same subjects without the problems behind the comparison of different populations. We are currently expanding this approach by collecting diffusion tensor imaging data on the same individuals in order to examine the anatomical basis for the pattern of actions reported in this thesis (Cerliani et al., in prep)

Shared circuits

Reading my thesis you will notice that I start with writing about a human mirror neuron system to progressively move to use the more general term of shared circuits. This change of terms is a consequence of the fact that fMRI and single cell recordings have a very different resolution: while single cell recordings cannot test all the cells in the brain, fMRI still cannot isolate the activity of a single neuron. In fact, we cannot differentiate whether a particular fMRI voxel, found to be involved in action observation and execution, contains neurons with mirror properties or instead, contains two distinct but intermixed populations of neurons, one responding only during action observation and the other only during action execution. The only way to disentangle these alternative possibilities would be to directly record the properties of the neurons in that specific voxel. While this problem remains unresolved, for fMRI experiments in human, to avoid misinterpretation, we would suggest switching from speaking of mirror neuron system to the more general terms shared voxel and share circuit. The recent introduction of fMRI in monkeys, that permits a better comparison between the two species, some rare case of

[1] The order of the chapters in this thesis does not always reflect the chronology of my work. In particular, chapters 1 and 2, that act as an introduction into the MNS have been written half way during my PhD and therefore already incorporate some of the experimental work I will present in later, empirical chapters.

implanted electrodes in humans (Hutchison et at, 1999) and the speed at which technology proceeds give me hope that one day will be able to ascertain a definition based on the property of individual cells in both humans and monkeys, bridging the unfortunate gap between the two species.

Overlap in fMRI

In monkeys, a crucial property for a neuron to be classified as mirror is the 'duality' of its discharge: significant during the execution and during observation and/or listening of an action. To be consistent, we consider a voxel as shared voxel only if it is activated by the execution/experience *and* by the observation/listening of a similar action/sensation.

Goals

When writing of actions, in this manuscript, we will often refer to *what has been done* as the *goal* of the action, even if it might not always be the perfect word to use. Some definitions of the word *goal* include aspects of an action that our data does not address. The intentionality of an action, for instance, is one of these aspects. The use of the term goal is, on the other hand, quite intuitive and simpler than a wordier phrase like 'what a movement tries to achieve' and this is why we are still using it even if imperfect. Why do we not look for a better word? Because we believe there are still many experiments to be run, before understanding what aspects of an action are truly translated by the mirror neuron system: only then will the data provide a clearer understanding and a better word might emerge.

References

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